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**Hypoxia in the Holocene Baltic Sea: comparing modern versus past intervals
using sedimentary trace metals**

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Highlights (max. 5 ÷ max. 125 characters each)

- ◀ Holocene Baltic Sea sediments from hypoxic intervals are enriched in trace metals.
- ◀ The strongest enrichments in U are observed in recent sediments, indicating that modern oxygen depletion is most intense.
- ◀ Lower Mo in recent sediments compared with C_{org} and U, suggests depletion of the present-day water column Mo inventory.
- ◀ Enrichment of Re commences under mildly reducing conditions, but Re is not further enriched under more reducing conditions.
- ◀ Ni, Tl and Cu correlate with C_{org}, while Pb, Zn, As, Sb and Cd are all strongly influenced by anthropogenic pollution.

Abstract

Anthropogenic nutrient input has caused a rapid expansion of bottom water hypoxia in the Baltic Sea over the past century. Two earlier intervals of widespread hypoxia, coinciding with the Holocene Thermal Maximum (HTM_{HI}; 8-4 ka before present; BP) and the Medieval Climate Anomaly (MCA_{HI}; ~1200–750 years BP), have been identified from Baltic Sea sediments. Here we present sediment records from two sites in the Baltic Sea, and compare the trace metal (As, Ba, Cd, Cu, Mo, Ni, Pb, Re, Sb, Tl, U, V, Zn) enrichments during all three hypoxic intervals. Distinct differences are observed between the intervals and the various elements, highlighting the much stronger perturbation of trace metal cycles during the modern hypoxic interval. Both Mo and U show a strong correlation with C_{org} and very high absolute concentrations, indicative of frequently euxinic bottom waters during hypoxic intervals. During the modern hypoxic interval (Modern_{HI}) comparatively less Mo is sequestered relative to C_{org} than in earlier intervals. This suggests partial drawdown of the water column Mo inventory in the modern water column due to persistent euxinia and only partial replenishment of Mo through North Sea inflows. Molybdenum contents in modern sediments are likely also affected by the recent slowdown in input of Mo in association with deposition of Fe and Mn oxides. Strong enrichments of U in recent sediments confirm that the Modern_{HI} is more intense than past intervals. These results suggest that U is a more reliable indicator for the intensity of bottom water deoxygenation in the Baltic Sea than Mo. Sedimentary Re enrichment commences under mildly reducing conditions, but this element is not further enriched under more reducing conditions. Enrichments of V are relatively minor for the MCA_{HI} and Modern_{HI}, possibly due to strong reservoir effects on V in the water column, indicating that V is unreliable as an indicator for the intensity of bottom water

hypoxia in this setting. Furthermore, Ba profiles are strongly influenced by post-depositional remobilization throughout the Holocene. The strong relationship between C_{org} and Ni, Tl and particularly Cu suggests that these trace metals can be used to reconstruct the C_{org} flux into the sediments. Profiles of As, Sb and Cd and especially Pb and Zn are strongly influenced by anthropogenic pollution.

Keywords (max. 6)

Redox conditions, anthropogenic pollution, aqueous trace metal depletion, molybdenum, uranium

1. Introduction

Sedimentary trace metal records have widely been used as proxies for productivity and redox conditions in both modern and ancient aquatic systems (e.g. Calvert and Pedersen, 1993; Morford and Emerson, 1999; Tribovillard et al., 2006; Brumsack, 2006). Sedimentary trace metal concentrations are often low under a well-oxygenated water column (e.g. McLennan, 2001), while under low-oxygen conditions their concentrations are generally elevated due to the interplay of several related processes (e.g. Tribovillard et al., 2006).

Trace metals are closely associated with organic material in both the water column and in sediments (e.g. Pedersen and Calvert, 1990; Canfield, 1994; Tribovillard et al., 2006). Under well-ventilated conditions, only a fraction of the organic-bound trace metals in the water column reaches the sediment-water interface, due to efficient remineralization of organic matter in the water column. Under low-oxygen conditions, however, less organic material is remineralized leading to an

76 increase in the direct input of organic-bound metals to the sediments. Sediments are
77 further enriched in trace metals under these conditions through uptake of trace metals
78 by organic matter at the sediment-water interface.

79
80 A second key vector of trace metal transport to sediments is via Mn- and
81 Fe(oxyhydr)oxides. Many trace metals are adsorbed onto oxide particles, which are
82 highly mobile in seafloor environments where variable redox conditions lead to
83 repeated cycles of dissolution and re-precipitation (e.g. Froelich et al., 1979; Shaw et
84 al., 1990; Tribovillard et al., 2006). These processes can lead to the focusing of trace
85 metals into defined areas of the seafloor (e.g. Lenz et al., 2015a). Although trace
86 metal enrichment may occur under well-oxygenated conditions when metal-bearing
87 Mn- and Fe-oxides are preserved in the sediments (e.g. Schaller et al., 2000), a more
88 common route of enrichment is that metals are released during dissolution of oxides in
89 the surface sediments, and subsequently sequestered in organic matter, sulfide
90 minerals or other reduced authigenic phases (Morford and Emerson, 1999;
91 Tribovillard et al., 2006).

92
93 A third pathway for trace metal enrichment is related to diffusive transport
94 from seawater into sediments and subsequent sequestration in association with
95 organic matter or authigenic minerals. Depending on the metal, enrichment may
96 commence at various stages of bottom water oxygen depletion, i.e. the metal may be
97 sequestered under hypoxic (dissolved oxygen concentrations < 2 mg/L), anoxic (no
98 dissolved oxygen) or euxinic conditions (no dissolved oxygen and presence of free
99 sulfide) (Crusius et al., 1996; Tribovillard et al., 2006; Olsson et al., 2017).

100

Two of the most studied and widely applied redox-sensitive trace metals, Mo and U, have many properties in common (see Algeo and Tribovillard, 2009 for an overview). One key difference between Mo and U is that the presence of free sulfide is a prerequisite for Mo enrichment in sediments. Sulfide is required to convert relatively unreactive seawater molybdate to particle reactive thiomolybdate (Helz et al., 1996). In contrast, authigenic U sequestration, primarily precipitated as uraninite (UO₂), already commences when Fe (III) is reduced to Fe (II) (Zheng et al., 2002), making U a potentially more sensitive recorder of minor changes in bottom water oxygen conditions. Another key difference is that water column Mo is actively scavenged by particle Mn- (and sometimes Fe) oxides, which may carry Mo to the sediment-water interface (e.g. Turekian, 1977; Adelson et al., 2001; Sulu-Gambari et al., 2017), whereas U is generally enriched via diffusion into sediments (e.g. Klinkhammer and Palmer, 1991). These differences in the sequestration of Mo and U can be used for detailed reconstructions of depositional conditions (Algeo and Tribovillard, 2009). In addition, the strong relation between C_{org} and Mo in euxinic environments can be used to identify basin reservoir effects, i.e. the depletion of an element in the water column of a stagnant basin through removal of that specific element to the sediment in excess of resupply by deepwater renewal. In this manner, aqueous Mo may become depleted, resulting in lower sedimentary Mo/C_{org} ratios (Algeo and Lyons, 2006).

Besides Mo and U, Re and V are the most studied and widely used redox-sensitive trace metals (e.g. Morford and Emerson, 1999; Morford et al., 2005). The low crustal abundance of Re results in relatively large, and therefore very distinctive, authigenic enrichments under reducing conditions (Koide et al., 1986; Crusius et al., 1996; Böning et al., 2004). Unlike for instance Mo, Re does not show an affinity for

Mn- and Fe-oxides and is sequestered in sediments under suboxic conditions after diffusion across the sediment-water interface (e.g. Colodner et al., 1993; Morford et al., 2012). Under well-oxygenated conditions V (in the form of vanadate oxyanions) adsorbs onto Mn- and Fe-oxides (e.g. Wehrli and Stumm, 1989), but is also strongly associated with organic matter (e.g. Beck et al., 2008), so both may be important carriers of V to deeper waters or the sediment-water interface. Under moderately reducing conditions, V(V) is reduced to V(IV), which is more surface reactive and more easily complexes with (in)organic ligands (Emerson and Husted, 1991). This may lead to enhanced sedimentary V sequestration, but the complexation of V(IV) with dissolved organic matter may also allow it to remain in the aqueous phase (e.g. C D 7 c b b c f ' Y h ' U ` " ž ' & \$ % + . In contrast with for instance Mo, UV " ž ' & \$ % + sequestration is not linked to the formation of authigenic sulfides (Algeo and Maynard, 2004). However, under euxinic conditions V can be reduced to V(III), which enables V sequestration through the precipitation of vanadium(hydr)oxide (Wanty and Goldhaber, 1992).

A prime example, and perhaps the most widely used trace metal to reconstruct marine primary productivity, is sedimentary Ba, which largely reflects biogenic barite (BaSO_4), a remnant of decayed organic matter that is preserved in sediments (Bishop, 1988; Dymond et al., 1992; Schoepfer et al., 2015). The applicability of sedimentary Ba as a (paleo)productivity proxy seems to be limited to open ocean settings, for example, because a certain water depth (~1000 m) is needed in order to fully develop the barite-productivity signal settings (Von Breymann et al., 1992; Plewa et al., 2012). Its applicability is further complicated by remobilization of Ba under reducing conditions (e.g. McManus et al., 1998; Henkel et al., 2012). Despite these

complications Ingri et al. (2014) showed that sedimentary Ba may represent primary productivity in the Bothnian Bay during the last 5.5 kyr.

Furthermore, trace metal enrichments are also used to assess anthropogenic pollution in (semi)modern sediments (e.g. Caccia et al., 2003; Ip et al., 2007). Many trace metals have applications in agriculture and industry, e.g. in fertilizers, pesticides, pigments and lubricants. These trace metals can be transported to the oceans by fluvial and eolian pathways, where they are sequestered in sediments after adsorption onto clay particles and (oxyhydr)oxides and complexation with organic compounds (e.g. Nriagu and Pacyna, 1988; Windom et al., 1989; Liaghati et al., 2004).

The Baltic Sea is an ideal location to assess how changes in bottom water oxygen, primary productivity and anthropogenic pollution are recorded by trace metals in marine sediments. Its geographic configuration, i.e. landlocked with a restricted connection to the open ocean (Fig. 1a), in combination with excessive anthropogenic nutrient input (e.g. Gustafsson et al., 2012), has resulted in a tenfold increase of the hypoxic area over the past century (Carstensen et al., 2014), creating the largest human-induced hypoxic area in the world (Diaz and Rosenberg, 2008). The modern Baltic hypoxic interval (henceforth Modern_{HI}), was preceded by two previous hypoxic intervals during the Holocene (Zillén et al., 2008). The first hypoxic interval coincided with the Holocene Thermal Maximum (HTM_{HI}; ~8 and 4 ka before present - BP). The second interval of widespread hypoxia in the Baltic Sea coincided with the Medieval Climate Anomaly (MCA_{HI}; ~1200–750 years BP).

The laminated sediments marking the hypoxic intervals in the Baltic Sea are characterized by high organic carbon (C_{org}) and molybdenum (Mo) contents (Jilbert and Slomp, 2013a; Dijkstra et al., 2016; Hardisty et al., 2016; Papadomanolaki et al., 2018), indicative of free sulfide in bottom waters (Helz et al., 1996). Previous studies have drawn various conclusions about the environmental conditions during each of the hypoxic intervals. High-resolution records of Mo enrichment indicate that the development of the Modern_{HI} was more rapid than the development of the MCA_{HI} and HTM_{HI}, while the maximum intensity of hypoxia was similar for all three events (Jilbert and Slomp, 2013a). In contrast, Hardisty et al. (2016) concluded, based on Mo isotopes, that reducing conditions during the MCA_{HI} and HTM_{HI} were probably more intense than during the Modern_{HI}. Focusing on the areal extent, rather than intensity, of hypoxia, Lenz et al. (2015a) concluded on the basis of sedimentary Fe records that the present-day hypoxic area is larger than that in the past.

Here we present a comprehensive analysis of trace metal enrichments during the three hypoxic intervals from two sites in the central Baltic Sea. By considering a large number of trace metals together, we are able to test multiple hypotheses about the mechanisms of trace metal enrichment, and the suitability of trace metals for paleoenvironmental reconstructions in this setting. Specifically, we investigate (1) the sensitivity of known redox-sensitive trace metal enrichments, i.e. Mo, U, Re and V, to variable redox conditions, (2) which trace metals may be reliable proxies for the organic carbon (C_{org}) flux into the sediments and (3) the effect of anthropogenic pollution on sedimentary trace metal records. We have generated complete discrete-sample records of 13 trace metals (As, Ba, Cd, Cu, Mo, Ni, Pb, Re, Sb, Tl, U, V, Zn), as well as major and minor sediment components (Al, Fe, S, C_{org}), for the entire

sediment column spanning the three hypoxic intervals and the intervening oxic periods, at two sites in the Baltic Sea (Fig. 1). Additionally, we present Laser Ablation-Inductively Coupled Plasma-Mass Spectrometry (LA-ICP-MS) line-scan Mo and U data for the three intervals at one of the two study sites. The LA-ICP-MS records allow an orders-of-magnitude increase in the depth resolution of the trace metal profiles, facilitating robust analysis of relative enrichments between Mo and U, and investigation of how the two elements respond to short-timescale changes in oxygen conditions.

2. Materials and methods

2.1 Study site

Sediment samples were retrieved from two different localities in the central part of the Baltic Sea during two research cruises with *R/V Aranda* in May-June 2009 and August 2013. Multicores (0-35 cm below seafloor; cmbsf) and gravity cores (~25-440 cmbsf) were collected from site F80 in the Fårö Deep (58.0000°N, 19.8968°E, 191 m water depth) and from site LL19 in the Northern Gotland Basin (58.8807°N, 20.3108°E, 169 m water depth; Fig. 1) in 2009. An additional short core (0-55 cmbsf) was taken at site F80 in 2013 with a GEMAX corer.

2.2 Processing of the sediment cores

The multicores and GEMAX core were sliced on board the ship under an oxygen-free atmosphere at in-situ bottom water temperature. The resolution of the sediment slices was 0.5 cm for 0-2 cmbsf, 1 cm for 2-10 cmbsf and 2 cm from 10 cmbsf until the bottom of the core. The GEMAX core for F80 retrieved in 2013 was sliced under the same conditions but with a resolution of 1 cm for the samples

analysed in this study (0-10 cmbsf). The gravity cores were stored at 4°C and sliced under an oxygen-free atmosphere in the laboratory at Utrecht University at a resolution of 1 cm. All sediment samples were freeze-dried and weighed before and after freeze-drying in order to determine the water content and to calculate porosity. The samples were subsequently powdered and homogenized using an agate mortar and pestle in an oxygen-free atmosphere.

2.3 Organic carbon content

Organic carbon content data (C_{org}) for the 2009 cores was generated and published by Jilbert and Slomp (2013a). For the 2013 GEMAX core 0.1-0.2 g of freeze-dried and powdered sediment sample was weighed in 15 ml centrifuge tubes and 7.5 ml of 1M HCl was added to dissolve carbonates. After four hours on a shaker the acid was removed through centrifugation and fresh 1M HCl was added after which the samples were left on a shaker overnight. The acid was then removed again after centrifugation and samples were washed twice with milliQ water, and dried at 60°C for 72 hours. The dried residues were then weighed again to determine the weight loss. Finally, the samples were powdered and homogenized and ~5 mg of each sample was weighed in a tinfoil cup. Total carbon analyses were performed using a Fisons Instruments NA 1500 NCS analyzer. Obtained results were normalized to in-house standards, acetanilide, atropine and nicotinamide. An internationally certified soil standard (IVA2) was measured after each 10 samples to determine the accuracy and precision of our analyses. The certified value for IVA2 is 0.732 wt.% C, our obtained mean value was 0.726 wt.% C with a standard deviation of 0.014 wt.% C. Finally, C_{org} was calculated upon correction for the weight loss due to the decalcification. An

average analytical uncertainty of 0.08 wt.% was calculated based on duplicate analyses of sediment samples.

2.4 Trace metal concentrations

For the determination of sedimentary trace metal concentrations about 125 mg of freeze-dried and powdered sediment sample was weighed in 30 ml Teflon vessels. Subsequently 2.5 ml of mixed acid ($\text{HClO}_4\text{:HNO}_3$, 3:2) and 2.5 ml 40% HF were added and the vessels were left overnight on a hotplate at 90°C. The following day the lids of the vessels were removed and the extracts were heated to 140°C to evaporate the acids. The remaining residues were then dissolved in 25 ml 4.5% HNO_3 and left overnight on a hotplate at 90°C again. The dilution of the final solutions was determined by weighing the vessels, after which the solutions were analysed by Inductively Coupled Plasma-Optical Emission Spectrometry (ICP-OES; Al, Fe and S published previously in Jilbert and Slomp, 2013a and Lenz et al., 2015a) and by Inductively Coupled Plasma-Mass Spectrometry (ICP-MS; As, Cd, Cu, Mo, Ni, Pb, Re, Sb, Tl, U, V and Zn). For the latter analyses, we used an XSeries II ICP-MS (Thermo Fisher Scientific) equipped with a Peltier cooled, low-volume conical spray chamber fitted with a micro nebulizer, a micro pump and a FAST system on the autosampler (SC-4 DX; Elemental Scientific), to enhance stability, enable fast washout and minimum cross contamination and optimize sample throughput. The accuracy (recovery) was generally between 95 and 105% for all reported elements based on in-house standards. The average analytical uncertainty based on duplicates, in-house standards and laboratory reference material (ISE-921) was 2% for As, 1% for Cd, 2% for Cu, 1% for Mo, 2% for Ni, 2% for Pb, 8% for Re, 2% for Sb, 4% for Tl, 2% for U, 2% for V and 2% for Zn.

2.5 Resin Embedding and LA-ICP-MS

Sections of the sediment cores from F80 (2009 gravity core and 2013 GEMAX core) were prepared for LA-ICP-MS analysis by resin embedding. From the gravity core, U-channels of sediment (20 x 2 x 1 cm) were sampled horizontally from the open core surface as described in Jilbert et al. (2008) and transferred immediately to an N₂-filled glovebox. A total of 180 cm of sediment, including the laminated intervals corresponding to the MCA_{HI} and HTM_{HI}, were sampled in this way. From the GEMAX core, a vertical column of miniature sub-cores of sediment (8 sub-cores in total, each 1 cm diameter, 7 cm length) was taken as described in Jilbert and Slomp (2013a). The entire sub-coring operation was performed in a N₂-filled glove bag and the sub-cores were transferred to an N₂-filled glovebox. All U-channels and sub-cores were then dehydrated with argon-purged acetone, fixed in SpurrD epoxy resin, and sliced to reveal the interior surface using a water-cooled rock saw. The interior surfaces were polished prior to subsequent analysis.

Resin-embedded sediment blocks were mounted in the ablation chamber of the LA-ICP-MS instrument at Utrecht University. The ablation chamber sits on a mobile stage. Line scan profiles were generated by focusing a pulsed argon-fluoride excimer laser beam (120 µm spot size, 193 nm wavelength, 10 Hz repetition rate, 8 J cm⁻² energy density) onto the moving sample surface and ablating material into a high mass-resolution ICP-MS (Thermo Element 2) via a He-Ar carrier gas. During line scans the stage velocity was optimized to 0.0275 mm s⁻¹ for high spatial resolution measurements (Hennekam et al., 2015). Count rates of the isotopes ²⁷Al, ⁹⁸Mo and ²³⁸U, among a range of other elements, were determined continuously at a measurement frequency of approximately 1 Hz.

The resin embedding procedure results in varying degrees of sediment compaction, such that the length of each line scan is less than that of the original U-channel or sub-core. To correct for compaction effects, the data from each LA-ICP-MS line scan was linearly re-scaled to the initial length of the sub-core. Subsequently, line scan data were fine-tuned by alignment to ICP-OES or ICP-MS data of discrete samples from the corresponding interval.

Raw LA-ICP-MS count data were converted to elemental compositional ratios via the two-step linear calibration procedure described in Jilbert and Slomp (2013a). Briefly, count rates of each element in the line-scan data were converted to preliminary concentrations using one-point sensitivity factors (counts/ppm) determined from a glass standard (NIST 610) at equivalent measurement settings. Preliminary concentrations of ^{98}Mo and ^{238}U were then normalized to ^{27}Al to correct for variable ablation yield during line scanning. The resulting ratios, corrected for natural isotopic abundances of each element, were further corrected using a linear regression against Mo/Al and U/Al concentration ratios of the equivalent sediment interval determined by discrete sample ICP-OES or ICP-MS analysis. This second step corrects for any offset between the sensitivity factors of the elements in the sediment sample relative to the standard glass.

2.6 Sediment chronologies

Age-depth models for the sediment cores used in this study were previously generated by Jilbert and Slomp (2013a) and Lenz et al. (2015a). For the present study we choose to show our data against depth instead of time. We have, however, included the dates, following Lenz et al. (2015a), in the supplementary data file. We follow Jilbert and Slomp (2013a) concerning the position of the Modern_{HI}, MCA_{HI}

and the HTM_{HI}. For the purposes of this study we do not discern different sub-events within the MCA_{HI} and HTM_{HI}.

3. Results

3.1 Trace metals in the Fårö Deep (site F80) and Northern Gotland Basin (site LL19)

The hypoxic intervals in the Fårö Deep are characterized by strong enrichments in sedimentary C_{org} (Fig. 2a). Maximum values are similar (~10 wt. %; Table 1) for the three hypoxic events when the top sediments consisting of fresh, non-degraded organic material, the so-called *Y X* *í Z* areileit zumf consideration. Both Mo and U are also strongly enriched in the sediments of all three hypoxic intervals (Fig. 2a; Table 1). Maximum values for Mo (>300 ppm) are recorded during the HTM_{HI}. Background Mo concentrations, i.e. in the intervening oxic intervals, are 25 ppm on average (Table 1). Uranium concentrations progressively increase from the HTM_{HI} to the Modern_{HI}, hence the present-day U concentration is the highest in the record. In contrast with C_{org}, Mo and U, Re shows rather constant concentrations throughout the studied sediment sequence, without significant enrichments during the hypoxic intervals (Fig. 2a; Table 1). Both V and Ba are strongly enriched during the HTM_{HI}, but not during other intervals, in particular the Modern_{HI}.

The profiles of C_{org} and trace metals for the Northern Gotland Basin site LL19 (Fig. 2b) largely resemble those for the Fårö Deep (Fig. 2a). Maximum C_{org} values for the three hypoxic intervals are slightly lower than in the Fårö Deep, i.e. around 8 wt. % (Fig. 2b; Table 2). Maximum values for Mo are recorded during the MCA_{HI} and HTM_{HI}, with somewhat lower maximum values during the Modern_{HI} (Fig. 2b). However, background Mo concentrations in the intervening oxic intervals (~6 ppm)

are much lower than in the Fårö Deep (Tables 1 and 2). Absolute U concentrations are also lower in the sediments of the Northern Gotland Basin, but the trend in U concentrations is the same as for the Fårö Deep, i.e. progressively increasing in the order $HTM_{HI} \rightarrow MCA_{HI} \rightarrow Modern_{HI}$. In contrast with the Fårö Deep, distinct enrichments in Re are observed during all three hypoxic intervals in the Northern Gotland Basin (Fig. 2b). Moreover, background Re concentrations in the intervening oxic intervals (10 ppb) are generally lower than in the Fårö Deep. Again, both V and Ba are strongly enriched during the HTM_{HI} , but strong enrichments are absent from the other intervals.

The other trace metals all show their strongest enrichments coinciding with the onset of the $Modern_{HI}$ (Fig. 3a). Significant enrichment in Zn is entirely confined to the $Modern_{HI}$, while for Pb there is also a small enrichment towards the end of the MCA_{HI} , followed by a rapid drop and a gradual increase towards the $Modern_{HI}$ (Fig. 3a). For Sb and As we observe both a strong $Modern_{HI}$ -related enrichment and moderate enrichments during both the MCA_{HI} and HTM_{HI} , which generally follow the profiles of S and Fe (Fig. 3a). Enrichments in Cd, Ni, Tl and Cu are more similar to those of C_{org} and Mo. Even the smaller variations in C_{org} and Mo, e.g. the maximum around 410 cmbsf (Fig. 3a), are clearly expressed, and the absolute magnitude of the enrichments in Ni, Tl and Cu is rather similar for all three of the hypoxic events.

As for the Fårö Deep, significant enrichment in Zn in the Northern Gotland Basin is confined to the $Modern_{HI}$, while for Pb there is also a small enrichment visible towards the end of the MCA_{HI} . For Sb, As, Cd, Ni, Tl, and Cu, there are, besides the strong $Modern_{HI}$ -related enrichment, clear enrichments visible during both

the MCA_{HI} and HTM_{HI} (Fig. 3b). The magnitude of the enrichments in Ni, Tl and Cu is again similar for the three different hypoxic intervals, while for Sb, As and Cd, the enrichment during the Modern_{HI} is much larger than the enrichments during the MCA_{HI} and HTM_{HI} (Fig. 3b).

3.2 High-resolution molybdenum and uranium records

Trends in the high-resolution Mo and U LA-ICP-MS data for each of the hypoxic intervals in the Fårö Deep (Fig. 4) are in good agreement with the results for the discrete samples (Fig. 2a). However, the LA-ICP-MS data reveal significantly more internal variability within these intervals, and rapid changes in enrichment as previously demonstrated by Jilbert and Slomp (2013a) for shorter sections of the Holocene record. Moreover, the LA-ICP-MS data clearly show that U enrichment increases gradually at the onset of centennial-scale hypoxic intervals, while Mo enrichments increase rapidly beyond a certain point in the development of each event.

The contrast between relative Mo and U enrichments in each hypoxic interval is further illustrated by the LA-ICP-MS data. Although both elements are clearly enriched in all intervals, the Mo/U ratio differs markedly between HTM_{HI}, MCA_{HI} and Modern_{HI}. In hypoxic events within HTM_{HI}, Mo/U oscillates around 10, while in MCA_{HI} the average value is close to 5, and for Modern_{HI} the average value is close to 3.5 (Fig. 4).

4. Discussion

4.1 Molybdenum and uranium as proxies of bottom water redox conditions

The extremely high concentrations of Mo during the three hypoxic intervals can only be explained by persistent euxinic conditions at these times (e.g. Scott and Lyons, 2012), as concluded by previous studies of Baltic Sea sediments (Jilbert and Slomp, 2013a; Dijkstra et al., 2016). The similar maximum values of C_{org} and Mo for the three hypoxic intervals have previously been interpreted to indicate that the intensity of hypoxia during each interval was similar (Jilbert and Slomp, 2013a). However, the increase in U concentrations from the HTM_{HI} to the $Modern_{HI}$ observed in our new data causes us to reassess this conclusion. Taken alone, the U records suggest that the intensity of the hypoxic intervals has in fact increased towards the present day. This would imply that increased anthropogenic nutrient inputs to the Baltic during the 20th century (e.g. Gustafsson et al., 2012; Carstensen et al., 2014) have led to a perturbation of trace metal cycling that exceeds the natural variability observed in earlier hypoxic intervals.

The average background Mo concentration of 25 ppm in the Fårö Deep suggests that even outside the hypoxic intervals, bottom waters in this location may have been intermittently euxinic (Scott and Lyons, 2012). The lower average background Mo concentration in the Northern Gotland Basin (6 ppm), although substantially above the crustal average (~1-2 ppm; McLennan, 2001), is significantly below that of the Fårö Deep, suggesting that sulfide remained restricted to pore waters (Scott and Lyons, 2012). This difference can be attributed to the greater water depth of the Fårö Deep (191 m versus 169 m), making it naturally more susceptible to deoxygenation. The relatively early onset of U enrichment compared to Mo during short-timescale hypoxic events within the HTM_{HI} , MCA_{HI} and $Modern_{HI}$ in the Fårö

'DQHOL\D %RUHRP\VLQDH LQ WKH \$XV

WHOVRQ ODWHUDO PDUJLQV KDYLQD [LOOLSHG IRUF RSRGH VHJPHQW
VSLQLIRUB (B.) sphaerops DOG WKH WHOVRQ FROTHW PHELDO VHWDH %DVLV ZL
± RI WKH WHOVRQ (B.) sphaerops RI SOXPRGH VHWDH HQGLWH UDWKH
ZKLFK QHHGV WR EH FRQUPHG FODOLQJRU LDFKHXPED ZLWKHONQUVVHW
D VLPLODULW\ LQ WKH VKDSH RI ORQH FHD DSDAH [DEWH ULIRUK PDHUKO
ZLW (B.) sphaerops SDUWLFXODUO\ LQ WWRXWHGHQWHDRO WZLWK URXJK VHU
ODWHUDO DQB (B.) sphaerops RZSYOURY KDUDHWKHXPH HQGLWH VKRUW EXW ZH
SURGXFHG UR (B.) sphaerops RWMHLW HOUVRQ FUDHWH GXFHG LVFKLXP HQGLWH
ODFNLQJ DQWHULR (B.) sphaerops DQHSUXHVEROW HQW VHJPHQW WLPHV
WKH QDUURZHU DQWHQQDO VFDO SOXPRVH DQWHWHV DQWHV DQGHZDOHVHV
DJDLQVW B. (B.) sphaerops ZLWK ZHDNO\ VHWXORVH ODWHUDO

Description of holotype male \$QWHURGRUV DOG VHUUDWHG PHGLDO VHWDH 'DFV
RI FDUDSDFH ZLWK DFXWHO\ SRQDQWHG DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
URVWUXP ADQNHG E\ GLVWLQFW GLVWRPHQV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DQJOHV ODWHUDOO\ ZLWKRXW PGLVWRPHQV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
OREHV ODUJH WULDQJXODU SRLQDGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DEGRPLQDO VHJPHQW ZLWK EOXH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
SDUDFDXGDOLD THOVRQ WLPHV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VHJPHQW WLPHV DV ORQJ DV ZLGH SRVWHULRUO\ DV DQWHULRUO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DV ZLGH SRVWHULRUO\ DV DQWHULRUO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
OHQJWK ZLWK DERXW UDWKHU ORQJ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DEVHQW /DWHUDO PDUJLQV VOLJKWO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VHWDH LQFOXGLQJ IRXU WHUPLQDO VFKLXP ZLWK RYDO DQWHULRUO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DOWHUQDWHG E\ RQH ORQJ VSLQLIRUP WLPHV DV ORQJ DV PHUXV ZLWK
(\HV PRGUDWH LQ VLJH VOLJKWO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
ZLWK RYDO FRUQHD VOLJKWO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VWDON (\VWDON SDSLOOD SUHWHG UDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
SHGXQFOH VHJPHQW ZLWK ODUJH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VHJPHQW ZLWK WZR GRUVDO WXPVWHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DSLFDQ SURFHVV VHJPHQW ZLWK ODWHUDO SRVWHURGHV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
ORQJ SOXPRVH VHWDH RXWHU ADTHOQXP VHUUDWHG LQAD VHWGDQHPX
EDVLV ZLWK QXPHURXV ORQJ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
ODWHUDO VSLQH SHGXQFOH VHJPHQW DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DQG VHJPHQW GLVWRPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VHJPHQW GLVWDO PDUJLQ EURDGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VFDOH UDWKHU QDUURZ WLPHV DV ORQJ DV ZLGH SRVWHULRUO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
WZLFH DV ORQJ DV DQWHQQDO SHGXQFOH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
/DEUXP FRQLFDO ODQGLEOH QJHWH FRUSXV WLPVH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
LQFLVLXV DQG ODFLQLD PRELOLV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
HLJKW VHUUDWHG VHWDH SDUV SUDPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
PRODULV ZLWK JULQGLQJ SODWHV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
FRUSXV SURFHVVXV LQFLVLXV VRSUDV SODWH ODFLQLD PRELOLV ZL
ZLWK RYHU FXVSV SDUV FHQW SODPHS ZG WKIRSRG GLVWRPHQV DQGHG ZL
DPRQJ WKHP GLVWDO VHUUDWHG SDUV SUDPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
SDUV PRODULV ZLWK VHUUDWHG JULQGLQJ SODWHV DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VHJPHQW ZLWK UDWKHU ORQJ SOXPRVH VHWDH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
LV WLPHV DV ORQJ DV VHJPHQW WLPVH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
DQWHURPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VKRUWHU GLVWRPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
SRVWHULRU SOXPRVH VHWDH WKUHH SRVWHULRUO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
WZR VKLIWHG WR PHGLDQ PDUJLQ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
,QQHU UDPXV ZLWK YH ODWHUDO SURPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VL[DSLFDQ ORQJ VHWDH WKUHH SRVWHULRUO\ DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VLPLODU WR WKRVH RI PD[LOOD DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
([RSRG RYDO WLPHV DV ORQJ DV VHUUDWHG VRSUDV SODWH ODFLQLD PRELOLV ZL
HQGRSRG ZLWK SOXPRVH VHWDH VRSUDV SODWH ODFLQLD PRELOLV ZL
(QGRSRG VHJPHQW ZLWK DERXW DQWHURPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
SRVWHURPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
ZLWK ODWHUDO SOXPRVH VHWDH DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
HQGLWH QRWDEO\ SURORQJHG ZLWKHQHGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
SRVWHURPHGLDQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL
VLPLODU WR WKRVH RI PD[LOOD DQGHG E\ GLVWLQFW GLVWRPHQV DQGHG ZL

7KH VHTXHQFHV ZHUH QHDOU\VIDPHOWLSUDHOLRZLW K1 B9 FBI % (6 \$0
 GLYHUJHQFH EHWZHHQ WKHP 7KH PDODHGRVSKRZHQ UHODQDQ\DO\%DVV 6
 ORZ GLVWDQFH WR(BWspina)PTXHQFH RIWR f 6 f (± I
 FRPSDUHG WR D PXFK GHSHU 0D± GLVWDQFPHWR SUHYLRXV ,1 B9
 VSHFLHV RI WKH VXEJHQXV 7KH WZR VSHFLHVHQHGRVSKRZHQ UHODQDQ\DO\ \$
 PRUSKRORJLFDO VLPLODULW\ VHH &RPSDULVRQDERYH KRZHYHU
 D PRUH H[WHQVLYH WD[RQ DQG JHQHURVRSQDQ\WKRXVGRPHYHQRI FDU
 DFWXDO SK\ORJHQHWLF UHODWLRQWKLSV

Boreomysis (Boreomysis) siboga Hansen, 1910

) LJ

Boreomysis siboga+ DQVHQ SODWH , , DVJ DQWHULRUO\ 7HOVRQ ODWHUDO P
 D±H 2: 0 7DWWHUVD00 FHQWUDO SDUW ZLWK ± VSLQLIRUP
 1 LHUVWUDV] %UHQGHU j %UDQGLV VHUHV , VHWDH LQFUHDVLRQJ LQ OHQJ
 2 6 7DWWHUVD00 2: 0 7DWWHUVD00 VSLQLIRUP VHWDH ORQJHV
 2+ROPTXLVW ± WLPHV DV ORQJ DV VKRUWHU PH
 ± 2*RUGDQ 2%LUVWHLQ RI WHOVRQ OHQJWK ZLWKRXW
 7FKLQGRQRVD DERXW UDWKHU ORQJ VSLQXOHV (\
 ± 23LOODL PRGHUWH LQ VLJH EURDG VOLJKWO\
 0DXFKOLQH 0XUDQR 2)HQWU+DQVHQ SODWH , , R LKH B 2 ZLGWK FRUQHD VKRUW
 ± SODWH , , 2/DQFUDIW ORQJ DV VHQHQXODU SHGXQFOH H[WHQGH
 0•0OHU 23HWU\DVKRY D ORQJ DV ZLGH LWV GLVWRODWHUDO VS
 ± 2+DUJUHGYHV VSLQXOHV DSLFDOO\ ZLWK RQO\ VOLJK
 /RZU\ 6WRGGDUW 26DZDPRWR DQJOH QRW H[FHHGLQJ EH\RQG GLVW
 Boreomysis spinifera & RLIPDQQ SODWH , , 0 7DWWHUVD00 FDUSXV ZLWK VHYHQ PHGLD
 D±H SODWH 2J I J 2: 0 7DWWHUVD00 VHYJPHQWHG 3HUHRSRG SURSRGXV \
 > 1 Boreomysis spinifera 2+ROPTXLVW DV ORQJ DV VHYJPHQW 8URSRGDO H[R
 ± 2%LUVWHLQ 7FKLQGRQRVD VSLQLIRUP VHWDH RU
 @ VSLQLIRUP VHWDH RU

Type material 6\QW\SHV PDOH DQG VSLQLIRUP VHWDH RU
 f 6 f Siboga 5R QVQ 1 % & Body length ± PP
 & 586 (

Material)HPDOH LOOXVWUDWHG Comparison Boreomysis (B.) siboga V QRW NQRZQ \HV
 &RPPRQDOWK 0DULQH 5HVHUYH IURP KRYHDO\PDQLPXH PKODHWHUHV LQ WKH J
 WR f 6 f (± P (B) Bruce: 0 7DWWHUVD00 Boreomysis (B.) brucei
 FROO % 37 / () XJHV)XSULDQRYB (B) intermedia L Boreomysis (B.) brucei
 ,1 B9 B % (6 \$0 3 MXYHQLOH URYVWUXP VLPLODU WR WKH LPPD
 LOOXVWUDWHG 1HZ 6RXWK :DOHV DOG (B) siboga DQG WKHLU WD[RQRPLF VWDV
 f (WR f 6 f (± 5HPDUNVB (B) Boreomysis (B.) brucei
 3 FROO VDPH DV SUHYLRXV ,1 B9 B % (6 \$0 3 MXYHQLOH URYVWUXP VLPLODU WR WKH LPPD
 24 YRXFKHU % VXDGXOW PDOH URYVWUXP VLPLODU WR WKH LPPD
 MXYHQLOHV 1HZ 6RXWK :DOHV RU 5HPDUNVB (B) Boreomysis (B.) brucei
 f (WR f 6 f (± 5HPDUNVB (B) Boreomysis (B.) brucei
 0D\ FROO VDPH DV SUHYLRXV 1 Description of Australian specimens (adults) \$QWHURGRUVD
 3 VXDGXOW PDOH WHOVRQ &RPPRQDOWK 0DULQH 5HVHUYH IURP KRYHDO\PDQLPXH PKODHWHUHV LQ WKH J
 6RXWK :DOHV &HQWUDO (DVWHUQ &RPPRQDOWK 0DULQH 5HVHUYH IURP KRYHDO\PDQLPXH PKODHWHUHV LQ WKH J
 IURP f 6 f (WR f 6 f (± 5HPDUNVB (B) Boreomysis (B.) brucei
 ± P -XQ FROO VDPH DV SUHYLRXV 1 Description of Australian specimens (adults) \$QWHURGRUVD
 9 B % (6 \$0 3 MXYHQLOH URYVWUXP VLPLODU WR WKH LPPD
 +XQWHU &RPPRQDOWK 0DULQH 5HVHUYH IURP KRYHDO\PDQLPXH PKODHWHUHV LQ WKH J
 f (WR f 6 f (± 5HPDUNVB (B) Boreomysis (B.) brucei
 -XQ FROO VDPH DV SUHYLRXV 1 Description of Australian specimens (adults) \$QWHURGRUVD
 3 MXYHQLOH 7DVPDQLD %DVWUDWDOV (B) Boreomysis (B.) brucei
 f (WR f 6 f (± 5HPDUNVB (B) Boreomysis (B.) brucei
 0D\ FROO VDPH DV SUHYLRXV 1 Description of Australian specimens (adults) \$QWHURGRUVD
 \$0 3 MXYHQLOHV 1HZ 6RXWK :DOHV RU 5HPDUNVB (B) Boreomysis (B.) brucei
 &RPPRQDOWK 0DULQH 5HVHUYH IURP KRYHDO\PDQLPXH PKODHWHUHV LQ WKH J
 WR f 6 f (± P (B) Bruce: 0 7DWWHUVD00 Boreomysis (B.) brucei

'DQHOL\D %RUHRP\VLQDH LQ WKH \$XVV

Figure 4 Boreomysis (Boreomysis) sibogae (A, D–G, I–K) IHPDOH PP 7DVPD (B) L V X \$ D G XOW PDOH 1HZ 6
\$0 3 (C) MXYHQLOH 1HZ 6RXWK(H)DQXEDG\$003W PDOH 1HZ 6RXW KHDGH(D)DWH3JD
URVWUXP DQGCHURWWUDPHDQ(D)HKHVDGO(B)RSVNDHULRU PDUJLQFRSDEVRBHRU PD
RI DEGRPHQ DQG WHOVRQ ODWHUDG)SLVWHIRUPUSIDWVOPORWVHQRDQVSRDQ
HQQRSRG(K)YKQVSRDQDO H[RSRG PRVW RI VHWDH QRW VQRZQHV /PSHUHRSRG

[illegible]

'DQHOL\D %RUHRP\VLQDH LQ WKH \$XVW

2 6 7DWWHUVD00 B.(B.) spinifera QDignosis \$QWHURGRUVDO PDUJLQ RI F
&RLIPDQQ B.(B.) spinifera ZKLFK ZDV QRVW VWSB DWHKHU VKRUW DFXWHO\ SR
E\ +ROPTXLVW DQG %LUVWHULRU VWFKHQ BOREOMYSIDUHFKLQJ SUR[LPDO
EXW VXSSRUWHG E\ ,L 3LOODHJPHQDQG ABQWRQ E\HVOVROV KO\ URX
)HQWRQ LQ /RZU\ 6WRGGDUW& (\$FFRWGEOJ VORVORQJ DV ODV
RULJLQDO ;JXUHV RI &RLIPDQQ ± WKWLPDODV ORQJORQJLGH DQW
PDOH KDG D UDWKHU VKRUW URVWZLXPH SRVWGHULRU ZLWK DQWHSDSUOO
WKH DQWHQQDO VFDOH WLPHVFRQFORYH LQVFZHQWU DOKSIDXUR SZLOKO
HQGRSRG ZLWK WZR VSLQLIRUP VHOVHERWWH WHOLHUQ FOHWDZ LLQERKH
GLODWDWLRQ DQG WKH ORQJHVW DQGHVWKLQDHOWVSLQ QIRO R SLQW DRU R VM
WHOVRQ DERXW WLPHV DV ORQJVDWWKADQKHUWIEURPHG IRDORZPH HJURD
WKH DQWHULRU WKH\ ZHUH RQO\ GHWDHQJDERKWKGKDOI DV ORQJ DV FHO
E\ WKH VPDOOHU VLJH ORQJHU HRI SDOSVROO ODHQGVORQZLHWKWDQPHHQDR
VSLQLIRUP VHWDH \$W WKH FXUUHODWKHWDOR RJ RSLLQKORZOHBVH)WKL\$
LV LQGHG D UDWKHU VPDOO GLUHQSH DQGHK,WHQAD WWHQXSSRGRUWR
V\QRQ\PLJDWLRQ \$FFRUGLQJ WR VZKWLQOFXUWQDWHULRUWHU+BOBTZLGHW
WKH VSHFLPHQV IURP WKH IROVDFONRQHRISDSDOD VPDOO \$QW
ZKLFK VKH B.(B.) spinifera KDRG FOHDU GHULRUQVWLRQI RW DQWHQQDO VFDOH)
WKH DQWHULRU SDUW RI WKH WHOVRQ \$QWHULRU* 7KHV LWLPHW BKDOJDFWJH)
HLW B.(B.) spinifera RLB. VBR spinifera LQ LWV RVSDQDQRW DUPHG ZLWK DGGLWLRQ
VHQVH 'XH WR SRRU SUHVHUYDWLRQRI VHFHFKHQVLDQ DQFORY SRWWRPO
WR DVVLJQ WKHP WR DQ\ VSHFLHVEH)QPG \$SLVLRQDWHUDPDSLXQH 3HU
VSHFLPHQ XQB.(B.) spinifera QDP% LUVWHULRUQPHGLDO EXQFKHV SURSRGXV
&KLQGRQRYD SUB.(B.) spinifera \$QWHULRUQVWLRQV VHIJPHQW UDWKHU ORQJ
VHH GHWDLOV LQ WKH(B.) spinifera VORFVLBQ DERXW 8URSRGDO H[RS
7KH RYHUDOB.(B.) spinifera DQGRUWV ODWHULRU VSLQLIRUP VHWDH LWV SU
UHODWHG WD[D VWLOO UHPDLQU DQXWKH HQBWAIXQGRSRGXHLWR 2SRZ
SUHVHUYDWLRQ RI WKH VSHFLPHQSLQDQGPZLVW DHRUSKRORJLFD
YDULDWLRQ FRQFHUQLQJ WKH URVWXP H[HV DQWHQQDO VFDOHV DQ
XURSRGV Body length PP LPPDWXUH LQ \$XVW
± PP 1RUWK :HVW 3DFL;F

Boreomysis (Boreomysis) sphaeropsis 1964

)LJV

Boreomysis sphaeropsis L

± ;JV ± 20•OOHU

Boreomysis spinifera² % LUVWHLQ 7FKLQGRQRYD
;J

Type specimens ,L EDVHG KLV GHVULSWLRQD
ODUJH VHULHV RI VSHFLPHQV IURPZKLFK DQRPDOJZDV
GHVLJQDWHG DV 'WISH' DQG VKRXOGSURDEGQ DQWHULRUWHLR
KRORWISH -DSDQ 6KLJXRND 3UHIHFWXUH B.(B.) spinifera WKH
QHDU \$MLUR PLOHV >FD NP@ZHBV inopinata DQWHULRUWHLR
\$SU KDXO 1R (YHUWLFDO DQWHULRUWHLR B.(B.) spinifera
E DQG D PP IHPDOH ZDV GHVLJQDWHG DV B.(B.) spinifera
VDPH ORFDOLW\ ODU KDXQ WHOVRQ FOLWFRQJLQJWKH B.(B.) spinifera
1R 6WDWXV XQNQRZQ inopinata VS QRY DQG WKH VOLJKWO\

Type locality -DSDQ 6KLJXRND 3UHIHFWXUH WHULRUWHLR B.(B.) spinifera
LVOHW QHDU \$MLUR DERXW Nopopity WSRQRYV KLPD

Material)HPDOH VXEDGXOW PP Descriptions of Australian specimens \$QWHURGRUVDO
%\URQ %D\ IURP f 6 f R(FDU DSDFH ZLWK UDWKHU VKRUW
f (± P -XQ Investigator GSHUFWHG URVWUXP QRW UHDFKLQJ
%37 / (+XJKHU) . . .XSULDQRYDSHXQBFOH VHJPHQW ADQNHG E\ VF
9 B % (6 \$0 3 PDOH DQWHULRUWHLR PLQXWH FRQFD
GDPDJHG PP MXYHQLOH 1HULRUWHLR DQWHULRUWHLR
(DVWHUQ &RPPRQZHDOWK ODULQHVHULRUWHLR IZRVK fDSLFOO\ SRLQW
f (WR f 6 f (ZHOVRQ ± WLPHV DV ORQJ DV OD
-XQ FROO VDPH DV SUHYLRXV QHDLBQ\ BHDPK(6Q \$OWLS RI XURSRGDO
3 PDOH VXEDGXOW VDPH DV SUZLGRXQWUHLRUO\ DQG WLP
*HQ%DQN 24 YRXFKHU % DQWHULRUWHLR 7HOVRQ ODWHUDO PDU

5HFRUGV RI WKH \$XVWUDOLDQ 0XVHXP

9RO

Figure 5 Boreomysis (Boreomysis) sphaerops-F, H-N) VXEDGXOW IHPDOH 1HZ 6R(6)WKX EDG-KOV\$ OP B OH 1
6RXWK :DOHV \$Q K HDG GRUVDO DQWHQ(6) K EDG F DOBRSUNDHUI PR V S DUW RI DEGRPHQ
XURSRGV VHWDH (Q)SRVWHZLR GRUVDOCE)RS FVEGRPHQU(6)DAMRDDO DIO WFO OH GLVW
PLVV(Q)GLVWDO SDUW(H)IDCEWHE(Q)IDCEWHE ODU \$DOBIVS FVW B KE RUI JKW CPV Q GOEOR
GRU(M)SDUV FHQWUDOL(M)RPULLOV P (N)BVDHOLRU SRVWHULRU 6FDOHV PP \$±.

'DQHOL\ D %RUHRP\VLQDH LQ WKH \$XVV

Figure 6 Boreomysis (Boreomysis) sphaerops, XEDGXOW IHPDOH 1HZ 6R(XWRD: DOLVSH 3 HQGRSRG
(B) PD[LOOLSHG (C) SDWRSRU HQGRSRG DQWHULRU 6FDOHV PP

SDWS ZLWK ± VSLQLIRUP VHWDGHLVWURPHGLDOQSDERXZLVHKBXWHFRHFDY
VHWDH LQFUHDVLQJ LQ OHQJWK ZLWK LQ REXULVH DQG QGWWIRQH HUVHUPDQV
VSLQLIRUP VHWDH ORQJHVW WHUSFLQDO PRGQ; FRUPLQWD RI
HQWLUH WHOVRQ OHQJWK ADQNHG HEUHQSRGDWH HEDGDZIGWKQH ± PHVGLDQH
VSLQLIRUP VHWDH KDOI DV ORQJZDWKFHQWQDGG&RXMMU FRUQHUI (QGR
WHOVRQ HQWLUH OHQJWK ZLWK VHYHVSLSRXWHU/LGLD VWVWHRQVFKHXFQW
(\HV ODUJH IURP GRUVD YLHZ ZLWK QKHVWRXQ ORQJ WSLWKMMO\ SOXP
ADWWHQHG GRUVRYHQWUDOO\ FRUQHUI RHGILDOZ PDUWKDQ BQGVWIRUWH
(\HVWON SDSLOD SUHVHQW UDWKHUUDPDODUJLW HGDZLVSKJXGFRH
ORQJHU WKDQ KDOI RI DQWHQDQH WDHORQ PHGLDOW QGLWKVUDWPDUI
GRUVRPHGLDO WXEHUFOH VHJPHRWRJLWSK WZRVGRUHDWHWXBHSGOZLV
RXWHU WXEHUFOH ZLWK DSLFDO SURFDHV VHFYKPEXQF FRGMDQLZLWKH
VHYHQ VHWDH DQG RQH SRVWHURGLVWRODWHQEKORV SOXPRV/OXPRWBH E
VHWDH RXWHU ADJHOXP YHQWVORQJLADHWUDVHGDQCEGLVWDZLWKQF
QXPHURXV ORQJ;QH VHWDH \$QLWVQDQFQHFQHERWK VHWPHQWV VHJP
DV ORQJ DV ZLGH DSLFDOO\ ZLWKRRQWKHMLJKVQDQJGKYBQFQGSXV V
GLVWRPHGLDO DQJOH SDUDGDFW\ODU\ VHWDH 8QJXLV WL
/DEUXP FRQLFDO ODQGLEOH DMKWUFHQSRGS/RGSURBHVLVWKLXP ZLWK
LQFLVLXYV DQG ODFLQLD PRELOLWHLXIR FXVSDWLPHS/DW FRQWUDVDEH
ZLWK HOHYHQ VHUUDWHG VHWDH SDUV SLDHPRODUJLPDQWK;QHVHWKH
SDUV PRODULV ZLWK JULQLQJ SOBHVDEGDUSSLV DQJXLW RI ±VHWWM
ULJKW FRUSXV SURFHVXV LQFLVLRVSRGDSHWRBGLDHLVRLQJ
ZLWK RYHU FXVSV SDUV FHQWOBQUDZLHVGSRSLDQGRUP WHVHVDV OR
DPRQJ WKHP GLVWDO VHUUDWHG SURFHVHPRDUDFXZLVKQJWKVZDQW
SDUV PRODULV ZLWK VHUUDWHG VHWDEGLQGRSBDQZDVKOSKQHLXPDVHWD
SDOS VHJPHQW ZLWK UDWKHU ORQJ SOXP RVH VHWDH VHW DSDUW
SUR[LPDQO\ DQG GHQVH GLVWDOO\ Variation PHW \$XVWUDVLPDQVSHORQV Z
DV VHJPHQW ZLWK;YH RU VL\ OBWKHODUJHUQXPRPHRIDWKBEKHQV
;IWHHQ ORQJ SUR[LPRPHGLDO DQG DERXWKDQKQWVKGLDWRPHBDWULD
VHWDH OD[LOOD 2XWHU UDPXV WKLWXYLQUDSRVHULRLOXPRAH V
VHWDH WKUHH RI WKHP JURXSHG DSDQDQVHGDQZPHWKHWPHGWRHQJ
PHGLDO PDUJLQ DSLFDO VSLQLIRUPKHVWBDQHUUDWHGPHQVSKXHU
ZLWK VHYHQ ODWHUDO IRXU SRVWHURQHVFPKGLDOLJKVQVHRH S
DSLFDO ORQJ VHWDH;YH DSLFD BIVKHDPGLWQDQVFRQDWHBFKLQD
WR WKRVH RI PD[LOOD DQG PD[LQDESHQ LQWKHVRUWKLOD 3DFL;F
([RSRG RYDO WLPHV DV ORQJZLVZLGHDERXVLRUPORQVHWDH RI WKH
HQGRSRG UHDFKLQJ LWV VHFRRQ RQJPHQWHLZLWK SOXP RVH DQGVDPH
(QGRSRG VHJPHQW ZLWK DERXW DQGDVHURPHGLDO DQGFRRXU
SRVWHURPHGLDO VHWDH VHJPHQW VSHLD WLPHVVRQKH \$XVZLGH
ZLWK ODWHUDO SOXP RVH VHWDH DQG DSLFDO VHUUDWHG VHWDH &RFDQ
HQGLWH QRWDEO\ SURORQJHG ZLWK GHQVH PDUJLQO\ DQG VSDQVH
SRVWHURPHGLDO VHWDH %DVDO HQGHVHYZLWK VLLRQJ VHUUDWHG VHW
VLPLODU WR WKRVH RI PD[LOOLSHG &DQDQGLWYH GXR YHUWLEDO VDP SOL
OD[LOOLSHG &R[D ZLWK WZR SOSHEVPHQGLDQSRVWHWDH%WKH 1RUWK
ZLWK SRVWHURODWHUDO SOXP RVH VHFRRQGRQVHWUDWGHQVSKXHU EDUH
UHDFKLQJ GLVWDO PDUJLQ RI LVEKXPGRQORQJ VHWVGHQVSKXHU
W\SHV WKLQQHU ORQJHU DQG AHLEOH EHORQJZLWK WKV VHSFschaebersDWKLV
VKRUWHU DQG VWRXW GLVWDOO\ ZLWK LKXVHUUDWLRQV DQG VSHD
OLNH DSH[3UHLVFKLXP HQGLWH VKRUW EXW ZHOO HVDQOLVKHG
FRPSDUHG WR UDWKHU UHGXFHG LVEKLPDQGHVH RQW &ZLWKORQPH V
SOXP RVH VHWDH OHUXV WKH ORQJHWRVHFWLQZBVYVBDQVSDQW IUI
ORQJ DV ZLGH ZLWK ORQJ SOXP RVH DQGVHUKLMDQVHVRZVHVRPH D
,VFKLXP DQG PHUXV ZLWK ZHDNQVWVXQHV &RQVULDQVDEKXV 'LY
&DUSRSURSRGXV WLPHV DV QSRFLAVPHWKXVZLWKQQRQZDV ±
SOXP RVH DQWHURODWHUDO DQG VHUUDWHG PHGLDO VHWDH 'DFW\OXV
RI FDUSRSURSRGXV ZLWKQXPRPHGLDOZLWKVORQJZLWYOLGHQVDOUDWKHU GH
VHWDH LWV GLVWRPHGLDO DQG SQGLVLPVPHGLDOZLWKPSDWUHWLHG
VHWDH 8QJXLV VWRQJ VHUUDWHG VHWG) obtusate DQWHORRVOHQRKHO\ UHO
OD[LOOLSHG ([RSRG VHJPHQWFRQWKM EMBDPSIDUWZLWQ;HG E\ %
EOXQW GLVWRODWHUDO DQJOH (QGRSRG) spinifer PDQVSRUSREUDVORQJ
VHWDWLRQ SDWWHUQ W\SLFDO SDHDDQVXEIDPLO\ &DUSRSURSRGXV

Figure 7 Boreomysis (Petryashovia) urosipina S QRY DOORW\SH IHPDOH PP \$0 3 6FDOH P
 * +ROPHV ZLWK SHUPLVVLRQ

ZLWK DERXW WR UDWKHU ORQDWSHUOROHV DQGV)LJWLPHV DV ZLGH
 ODUJH QHDOU\ JOREXODU ± &OHRW KHDBI ZLWKORQFRQVHWH OHQJWH
 GRPLQDWLQJ RYHU H\HVWDON HYBWSHSDOOPDDELVHQWH\$QVHQVWUDLUKW
 SHGXQFOH QRW H\WHQGLQJ EH\RQSDNDON\ EIUORWEGQQDOFQFLOCH)RXU WH
 ' \$QWHQQDO VFDOH)LJ ' - ¿MURWS\PHV DQFORQVLDQJ ZLGHJWK ORQJH
 DSLFDOO\ ZLWK RQO\ VOLJKWO\ DGYDQFHGGLVHWRHGGEDOODQJWK QDVN
 H\FHHGLQJ EH\RQG GLVWRODWHUDDG WZROPHGLDWHVQSLQOIBHBXQVMOCH
 ZLWK VOLJKW PHGLDO SURPLQHGFH\H\WZHUHGHVQPHVWVRXDOCHG ZLWK
 VHJPHQW QHDOU\ LQGLVWLQJXLWKDEVOBONLJH\HSDSHUORSRBEVHQW \$QW
 0 1 FDUSXV ZLWK VL[RU VHYHQ PGBUDDOEXQFQWV ZLWKSRODOKW GLVWF
 H[RSRG)LJ (ZLWK WKUHH OZWMKDDO EXSLQKLIRIUPHWHMDH\H\PHVQW
 SUR[LPDO VHJPHQW ± RI UDH\HOBQLRK (DSLFDQO\)ZLWK D EXQFK
 . ZLWK WKUHH WR ¿YH PHGLDO QSLQLOUTXDGUDDXODU IURP GRUVDQ V
 Body length RI IHPDOHV ± PP RI PDOHV V\PSRG ZLWK ODWHUDO VSLQH VHJPHQ
 WKDQ V\HJPHQW VHJPHQW UHGXFHG
 Comparison Boreomysis (P.) urosipina S QRY KDV FHHVHDOVHWDH VHJPHQW GLVWDO
 XQLTXH IHDWXUHV IRU WKH VXEJHQXVWKHDDOVBBOHPPUHWKROVZUEH
 KDV D PLQXWH FRQFDYLW\ RQ LWV DQWHQBBQSHGXQFQFK LV QRW NORZQ
 HYHQ DPRQJ RWBoreomysisVHFQMX QDWRDEWKHDSLFDQO\ QHDOU\ URXQGHG
 XURSRGDO H[RSRG LV UDWKHU ZLGHSHRHHV\XWKDQFLWYXV DQGVDFLQW P
 WR WHQ WLPHV DV ORQJ DV ZLGH FQWKKHQLVSHFWK\VH\WKHUXWHQVHWD
 EHDULQJ WKUHH VSLQLIRUP VHWDH\H\XQH\U\$ZVLPRQKHU ZLWKLUHQGL
 VHW QHDOU\ E\ WKH KDOI OHQJWKRIWKH\MD\XJKWFRUSXVDSBFWVQV
 RWKHU VSHBoreomysisVHFQVXQODWR DQGFWKHSDURSRGDO FHQWUDOLV ZLWK
 HQGRSRG LV ZLWK WKUHH RU ¿YH PHGLDOVSLQLIRUPVHWDHROGGLVWD
 WZR LQ RWKHU VSHFLB(P.) megalops ZLWKV\GHODUWVHV SDUV PRODULV ZL
 GLUHULQJ IURP LW LQ DGGLWLRQDQVPRHFDERYVSLQLIRUPVHWDHROGL
 FKDUDFWHUV E\ WKH ORQJHU DQWHQBBQVPRH\XPRHWHWDH\ZVHW DV
 ORQJ DV DQWHQBBQVPRH\XPRH\H\PHV DV ORQJ DV VHJPHQW ZLWK I
 PDOH SOHRSRGV ERB(P.) megalops DQWHQGLGLVWRPHGLDO DERXW ±
 DQG WKH WHOVRQ KDYLQJ ODUJHU DQPEHVKRIWKH\H\VLPDOGVBOQVHWDH
 VHWDH IRXU B(P.) megalops WZR LQ OD[LOOD 2XWHU UDPXV ZLWK DERXW
 VHWDH WKUHH RI WKHP JURXSHG PHGI
 Description of holotype male \$QWHURGRUVDFHPIIDUQIPDURILQ DSLFDO VSLQLIRUP VH
 FDUSDHF DQJXODU DSLFDOOZIEOKQVHODWHUDDOYHYZLQVHGDOKW
 FRQFDYLW\ DW HDFK VLGH DQWHQBBQVPRH\XPRH\H\PHV DV ORQJ DV VHJPHQW ZLWK I
 SRLQWHG 3RVWHURODWHUDO PDEH\OIRSHEGREGQDQOVVHDPHODW ([F
 DQJXODU DSLFDOO\ EOXQW RU ORQQCHGZLGH\H\VRECRXW DWLORQJDDV HQG
 ORQJ DV ODVW DEGRPLQDO VHJPHQWRSRGWLPHVH\H\PHV ORQVWQVDERXW DQ

'DQHOL\D %RUHRP\VLQDH LQ WKH \$XVV

Figure 8 Boreomysis (Petryashovia) urospinae (A-C) E-H, J, K) KRORW\SH PDOH (B, D, I) \$DOORW\SH IHP
PP \$0 3 (A, B) KHDG (G) KHDG (O) DMHJG OFDUDSDFH QER SRWKVIZQLR ODSVHWD BI D
WHOVRQ DQG XURSRGV VHWDH DQG V\$H QLRWPHVHWD FDRVLV QRI QFVG RPKRQ OQO
OHIW VLG(B) SRWKVIZQLR PDUJLQHRW BQV SRWKVIZQLR (S) DOQWR QV BQV RUKSRUGO
HQGRSRG YHQWUDO 6FDOHV PP

5HFRUGV RI WKH \$XVWUDOLDQ 0XVHXP

9RO

Figure 9 Boreomysis (Petryashovia) urospina S QRY KRORW\SH PDO(A) ODERUXP(B) HPOWGD XODU
SDOS SCYMHJKWUPDQG(DEFHIWPOWGLB)PH[YHODWU(F)SPVWLHULR U(G)RDMHODRSHG
DQWHHUGREW\ODU FODZI)RPHDI DOOLSHG RI PD[(J)EDSHGOL\$HCK)PHQWBLMHUUDW
VHWD RI PD[LOQL)SHGLDGFMMWXRI PD[LQ)LSHGHRSRGSRISQ)SSZHSRVRGHUEBUSX
DQW(K)PHGLDO VHWDH RI(P)PHGLDROGVHVDURV(Q)SHRSDGFWDUSXV(R)SDIQRUVSHUHF
ODWHUDO 6FDOHV PP \$±* - 0 1 5 + , . / 4 2 3

5HFRUGV RI WKH \$XVWUDOLDQ 0XVHXP

9RO

WKDQ H[RSRG ZLWK DERXW V[HSRUGDPB KLSVRGRSLFDO JH
ZLWK DERXW VHJPHQWV LWV QEHVQO R/HWKKHQRU QGW KQ WKRU WQW DUF
DQG VWURQJHU VSLQLIRUP VHWDGLMQRGRSRW H/K FVWFXUP WKO DUH RSRGWKH
ZLWK DERXW VHJPHQWV EHDULQORXQPWGH; H/GX WKWDDHG 30 HWRSG PHULFD
H[RSRG ZLWK DERXW VHJPHQWV EHDULQORXQPWGH; H/GX WKWDDHG 30 HWRSG PHULFD
H[RSRG ZLWK DERXW VHJPHQWV EHDULQORXQPWGH; H/GX WKWDDHG 30 HWRSG PHULFD
DERXW VHJPHQWV HQGRSRG VKWV H/HV K/DG HQR SRGKZ LWQDQ DHE RXW WKH
VHJPHQWV WKH \$XVWUDOLDQ UHJLRQ

8URSRGDO H[RSRG ZLWK WKUHH GLVWRODWHUDO VSLQLIRUP VHWDH
(QGRSRG ZLWK IRXU PHGLDO VSLQLIRUP VHWDH HSWK ±

Description of female \$QWHQXODU SHGX+DQOHVHJPHQW
VPDOOHU WKDQ LQ PDOH DOPRVW URXQG HG 0DUVXSIXP ZLWK VHYHQ
SDLUV RI RRVWHJLWHV \$OO SOH ERXUVH SHHG FENG WR VKBUW VHWRYH
SODWHV VHW RQ EDVDO VHJPHQW DQG ERDQ FVWFXUP WKO DUH RSRGWKH
SRVWHULRUO\ 8URSRGDO H[RSRG YRQ\ LQOHPRHV 6XKP 2KRLGH OXGHG
± WLPHV DV ORQJ DV HQGRSRG DQG WLPHV DV ORQJ DV HQGRSRG DQG
DV WHOVRQ LWV SUR[LPDO VHJPHQW WLPHV DV ORQJ DV HQGRSRG DQG

Colour 5HG)LJ ZDV DOVR WKH IDWH RI :LOOHPRHV 6XKP

Distribution and habitat 5HFRUGHG RQO\ IURP WKH GRXWKKHU GHV FULEHG WKH QHU
SDUW RI WKH 7DVDPDQ 6HD VRXV WDWRI 7DVDPDQ DV GHV FULEHG WKH QHU
± P)LJ 7KLW LV WKH PRVW ERUGHG SDUWV SHG FENG WR VKBUW VHWRYH
LQ WKH VXEJHQXV IRXQG DW WKH ERUGHG SDUWV SHG FENG WR VKBUW VHWRYH
EDWK\SHODJLF JRQHV HYDOXDWHG E\ WKH VWXGLHV RI WKH C

Molecular characters 7ZR QHDOU\ LGHQWLRUO\ 7KLQGHV RQRYD GHV FULEHG
B.(P.) uospina VS QRY IURP 7DVDPDQ LQOHPRHV 6XKP 2KRLGH OXGHG
GLVWDQW IURP HDFK RWKHU DQG %LUVWHLV H/HV K/DG HQR SRGKZ LWQDQ DHE RXW WKH
VSH Birsteiniamysis GHYHORSHG WKH FRQFDYLW\ ZLWK D Q

Neobirsteiniamysis Hendrickx et Tchindonova, 2020

Neobirsteiniamysis+HQGULFN[HW 7FKLQGRQRYD
+HQGULFN[XQDYDLODEOH WKH UHJLRQ :LWK WKH H[FOXVLRQ RI
+HQGULFN[7FKLQGRQRYD , XSGDWHG KHUHNH Birsteiniamysis LQ
Neobirsteiniamysis+HQGULFN[HW 7FKLQGRQRYD FRYDS DUL Birsteiniamysis LQ
2+HUQIQGH] 3D\iQ +HQGULFN[7FKLQGRQRYD SURSRVHG WKUHH

Birsteiniamysis 7FKLQGRQRYD ZLW Birsteiniamysis QHUPLV JURXS 6F\SKR
26WDU RI WKH =RRORJLFDO GRFLW Birsteiniamysis SUREDEO\ LQGLF
Birsteiniamysis 7FKLQGRQRYD GLUHHQWLDWLQJ ZLWK LQ WKH VSHFL
QRWLFHG DEVHQFH RI WKH WSHVSHFL ODUL\ WKH PHDQLQJ RI KHU SURSRVD
%HOLDHY Birsteiniamysis 7FKLQGRQRYD

3HWU\DVKRY D Birsteiniamysis DV DQ inermis \$PRQ\ WKHP RQO\ WKH ODW
7FKLQGRQRYD ZLWKRXW SXEOLFDFWLRQ LQ WKH \$XVWUDOLDQ ZDWHUV 7FKLQGRQRYD
Birsteiniamysis 7FKLQGRQRYD E UHIHUULQJ WR 7FKLQGRQRYD
Birsteiniamysis 7FKLQGRQRYD XQHVFULEHG VSHFLHV DQG VXEVSFL
Birsteiniamysis 7FKLQGRQRYD 6RXWKHUQ 2FHDQ DQG WKH FDVH VWLC
D Birsteiniamysis 7FKLQGRQRYD 6RXWKHUQ 2FHDQ DQG WKH FDVH VWLC
E /RZU\ 6WRGGDUW DV

Birsteiniamysis 7FKLQGRQRYD et al :LWWDQ

Birsteiniamysis 7FKLQGRQRYD

1RPHQ QXGXP

Birsteiniamysis 2+HQGULFN[2

+HQGULFN[7FKLQGRQRYD

3D\iQ +HQGULFN[5HIHUHG WR DV

XQDYDLODEOH QDPH

Neobirsteiniamysis inermis (Willemoes-Suhm, 1874)

2+HUQIQGH])LJV ±

Petalophthalmus inermis: LOOHPRHV 6XKP

D E * 2 6DUV D

Type species Petalophthalmus inermis: LOOHPRHV 6XKP

E\ VXEVSFLHVG GHV LQJQDWLRQ Petalophthalmus inermis: LOOHPRHV 6XKP

Petalophthalmus inermis: LOOHPRHV 6XKP

SDUWL IHPDOH RQO\

SDUWL IHPDOH RQO\ E SDUW

Diagnosis 7HOVRQ UDWKHU EURDG LQ WKH FVWFXUP WKO DUH RSRGWKH
RU ZLGHU WKDQ DQWHULRU SDUW Birsteiniamysis LQ OHPRHV 6XKP 2KRLGH OXGHG
ZLWK ODWHUDO FRQFDYLW\ D SODWH

Figure 11 Neobirsteiniamysis inermis IHPDOH
* +ROPHV ZLWK SHUPLVVLRQ

PP *UHDW \$XVWUDOLDQ %LJKW \$0 3

6

¿JV ± E SODWH ¿JV hanseni +ROPTXLVW
2)LOKRO 21RUPDQ Birsteiniamysis inermis27FKLQGRQRYD
2+DQVHQ ± ¿J ± 26WDu RI WKH =R
22UWPDQQ 26WHEELQJ 6RFLHW\ RI /RQGRQ 23HWU
2&DOPDQ 22KOLQ 2*HUVWDHF¿NHU± SODWH ± G D
2UWPDQQ ¿J ¿J E ¿JV D
2=LPPHU ± ¿JV ± ¿JV D
± 2+ROW : 0 7DWWHUVD00 2,0OLJ ± ¿JV ± E
26WHSKHQVHQ 2,0OLJ: LWWPDIQQ 2)XNXRND
21RXYHO 2=HQNJHUZLWFK% \$ & / 2:LWWPDQ
2(ORIVVRQ +DOOEHUJ 2. R X et al ¿J
¿JV \$ \$ ± 26WDu RI WKH =R Birsteiniamysis inermis found in
RI /RQGRQ et al DWKPDQ 2 QRP HQ QXGXP 26WDu RI WKH =RROR.
%UDWWHJDUG 0HODQG RI /RQGRQ ¿UVW PHQWLRQ DV
Boreomysis distinguenda+ DQVHQ ¿J Birsteiniamysis scyphos27FKLQGRQRYD ±
2: 0 7DWWHUVD00 UHPRYHG WKHUH IURP V\QRQ\PI 26WD
2=LPPHU 2,0OLJ =RRORJLFDO 6RFLHW\ RI /RQGRQ
Boreomysis inermis2: 0 7DWWHUVD00 Boreomysis inermis peruana% FHVFX ¿JV \$±
6 7DWWHUVD00 QRP HQ QXGXP
2+ROPTXLVW 2%LUVVHLBoreomysis scyphos3/HGR\HU
7FKLQGRQRYD ± ODSVXV FDODPL
¿J 2%LUVVHLQ 7FKLQGRQRYD Neobirsteiniamysis inermis2+HQGULFN[
± 20DXFKOLQH 0XUDQR 2+HQGULFN[7FKLQGRQRYD
20DXFKOLQH 2% FHVFX 3DiQ +HQGULFN[¿JV
¿JV> \$±DWKPDQ ¿JV
D±H 2/DXELW] et al /DQFUDIW Type specimens 3UREDEO\ ORVW
/HGR\HU 2 Type locality 6RXWKHUQ ,QGLDQ 2FHDQ QI
0•OOHU 2+DUJUHDYHV Material)HPDOH PP 6RXWKHUQ
2%UDQGW 2'H -RQJ ORUHDH \$XVWUDOLDQ %LJKW f 6 WR
&DVDQRYD &DVDQRYD \$XVWUDOLDQ %LJKW P \$SU
¿JV \$ % (\$ 20HODQG :LOODVVHQ WR f (± P \$SU
2&DVWHLLOODQL ¿JV 2±5 Investigator %37 \$ 0XUUD\) &ULVFL
1 Boreomysis inermis+ DQVHQ SO , , ¿J D±F 2,0OLJ 21RXYHO EHDP WUDZO \$0 3 VX
2+ROPTXLVW Boreomysis± PP MXYHQLOHV %DVV 6WUDLW

5HFRUGV RI WKH \$XVWUDOLDQ 0XVHXP 9RO

Figure 12 Neobirsteiniamysis inermis (A–F) IHPDOH PP *UHDW \$XVWUDOLDQ 0XVHXP IHPDOH %DV
\$0 3 (A) KHDG (B) RDVW (C) QQQXODU (D) GWHQFH (E) SYHQWUDORQ RXWHU ADJHOOXP RI
(D) DQWHQQXODU (E) SXURFHQD OGSDVWORF (F) SXURFHQD GRUWDR (G) DQWHQQD OYHGVOR
PP \$ % ' ± * &

'DQHOL\D %RUHRP\VLQDH LQ WKH \$XVW

Figure 13 Neobirsteiniamysis inermis (A–D, F) IHPDOH PP *UHDW \$XVWU(B)OVLDED&KJWWI\$PD3H %
\$0 3 (A) KHDG (B) DSRVUDULRU SDUQY SR VERIGULSR UPDUJ LQ(D) ISREGRPHQ UOPDW
DEGRPHQ (E) HCHVYK RSRGV YHQWUDO 6FDOH PP

Figure 14 *Neobirsteiniamysis inermis* IHPDOH PP *UHDW \$XVWU(ORDDQ%EXKOWUS\$H30SHIWRVWH
 PDQGLEO(C) BRILVDD (DSRVWUOLRU(ESDSWHDU RUHUUDWHG V(FWDSRFBD[V(OWD RHQO
 HQ(C)VPD[LOOLSH(H) ORQWSDXPUVH VHWD RI(PDKRQWSVIGUUDWHDG VHWGL RHPD[LQ
 6FDOH PP \$ % ' * ±, & ()

f (WR *f* (± P Comparison *Neobirsteiniamysis inermis*GLIIHUV IURP
 FROInvestigator %37 / (+XJKCM(U). *N. caeca* E\ WKH OHVV WUDQVSDUHQW FX
 .XSUL\DQRYD ,1 B9 B % (6 \$WUDQVSDUHQW OHVV SURWUXGLQJ
 Diagnosis 7HOVRQ)LJ % (± WLPHV DV ORQJ DV WKH HOVVRQ DWKHH BHHWHQIFQ
 ZLGH DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 FRQYH[ZLWK ± VSLQLIRUP VHWDH DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 WR WKUHH VKRUWHU FOHIW ± REWVH DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 PDUJLQV EHDULQJ ± VSLQXOHV DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 UHDFKLQJ GLVWDO PDUJLQ RI DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 KDOI RI VHJPHQW ODWHUDWOO\ ADWVH DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 KROORZ \$QWHQXODU SHGXQFOH)LJPHV DV ORQJ DV WKH HOVVRQ DWKHH BHHWHQIFQ
 UHDFKLQJ KDOI RI DQWHQXODU VFDH DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 DV ORQJ DV VHJPHQW \$QWHQXODU VFDH DQWHULRUO\ LWV ODWHUDW DQWHULRUO\ LWV ODWHUDW
 WLPHV DV ORQJ DV ZLGH DSLFDOO\ WUXQFEDWFG ZLWK DQWHULRUO\ LWV ODWHUDW
 GLVWRPHGLDO FRUQHU \$QWHQXODU SHGXQFOH WUXQFEDWFG ZLWK DQWHULRUO\ LWV ODWHUDW
 RI DQWHQXODU VFDH 8URSRGV ZLWK HIRSRG ZLWK HIRSRG ZLWK HIRSRG ZLWK HIRSRG
 ZLGH ± WLPHV DV ORQJ DV ZLGH RXWHU PDUJLQ ZLWK RQH WR
 WKUHH VSLQLIRUP VHWDH DW ±Description of Australian specimens (females) \$QWHULRU
 HQGRSRG)LJ) ZLWK RQH WR PDUJLQ ZLWK RQH WR PDUJLQ ZLWK RQH WR PDUJLQ

'DQHOL\D %RUHRP\VLQDH LQ WKH \$XVW

Figure 16 5HFRUGV RI WKH VSHFLHV RI WKH VXEIDPLO\ %RUHRP\VLQDH LQ \$XVWUDOL

ODWHUDO KROORZ RI WKH H\HV LQ WKH KRXVSHFLPHQV FHDORP%WKH VSHUQ
&KLOH 7UHQFK QRUPDOO\ UHG ZKLOH PDHFKYH%WHD RORPLF 6RXW
LPSRUWDQFH 7KH PD[LOOLSHG ODSURSGXVVDQGE BQZL WRXWKHUQ 2
ZLWKRXW WKH GLVWRPHGLDO FRQFOLWGR*GRYDDSKLFDO HUHUX.OHJLXMY
LQ WKH YDULDWLRQ KDV QRW EHHQ FRQWVWGHVW 3DFL;F Ru -DSDQ
UHFHQWO\ LQ WKH (DVW &HQWUDO 3
Molecular characters , ZDV QRW DEOH WR REWDLQ WHOLISURD +HUQIQGH] 3D\i
WKH \$XVWUDOLDQ VSHFLPHQV 7KHQ*HQH DQNUKROGVWKH FROVZLQXQ
JHQH IUDJN.therms VSHFLPHQV IURP FROVLOH QWDO VORSH IURP WKH &D
\$WODQWLF 6 U51\$ \$0 OHQDQHU:DOODV\$0HXWLDQ 5LGJH WF
PW'1\$ &2, 0. HQRODVH. XULO.DPPEDWND 7UHQFK f1)XN
6 U51\$ 0. etalRX , LQFRUSRQWKH GWHF IURP WKH 3HUX &KLOH
&2, VHTXHGFH LQWR WKH DQDO\VL\$QWDFWLFV)WKQW WR WKH \$QWDFW
IURP WKH &DQGLDQ %DVLQ WR WK
Distribution %LSRODU DPSKLWURSLFDQ VSHFLHV 2ULJLDQDGRBYD
GHVFULEHG IURP VXE \$QWDFWLF ZDWHUVWKH QGLDGRBYD
DQG WKH WURSLFDQ \$WODQWLF DQG 6RXWKHUL2FHDQSRUW4FHDQ
6XKP :LOOHP\HV 6XKP D %DV 2
6DUV D LW ZDV ODWHU GLVFRYDLDQW K%DIWK\$WODQWLF
* 2 6DUV E 2KOLQ +DQVHQLQGRQYDUHDYBMWU\DVKRY E
&DQDU\ %DVLQ 1RXYHO SVLQX:GRDEHVO6HD3HWU\DVKRY
7DWWHUVDQO /HGR\HU %QGV6FHRVQLD 7FHKD QRG RGRXYWK ED
\$WODQWLF et al/DQFUDI(VW 3DFL;F :HVWV3DSULQEHQWKLF EDWK\SHODJ
LQ %HULQJ 6HD DQG 2NKRWVN 6HEDQ:WKL7DWWHUQVQCHNWREHQWKLF K
H\WHQG HG IXUWKHU QRUWK IURP 3HWHU\ORXWK \$WODQWLE WRU 6SHKWK
*HRUJLD 2 6 7DWWHUVDQO etalKLQGRQRYDFLHV \$H5WK ±
3RODU %DVLQ %LUVWHLQ 7FKLZGRGRYD /RPNKQDGRQRYD
ODXFKOLQH 3HWU\DV SRWU\DVRYE ED ,Q \$XVWUDOLDQ
D +DUJUHDYHV 0XUDQR 6WHQRVXKFLJFDVHEQWKIR\$UFWLF EDV

5HFRUGV RI WKH \$XVWUDOLDQ 0XVHXP

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± f& WR ± f& 3HWU\DVKRY VSHFLPHQXW RHQHJHDSGPHG%VWUKLEVHG D
HXU\WKHUPDO VSHFLHV FDSDEOHGRICORWLQQLGLO WKHSURDQW HREH WZQVHQQ 1V
± f& DQG f& 3HWU\DVKRY DIRUQWKHUQ 1RQV KRSWCKHOMLFHPLVSKHU
IRXQG DW WHPSHUDWXUH RI ± f& ,ORK±V QDWHUH ZRURIW DEORWQRP GH
* 2 6DUV D %UDWWHJDUG VSHFLHV +DQVHQ WKH IURP WKH (D
1RUWK 3DFL;F DW WHPSHUDWXUHRSHGfLWVRQ \$UREYDPRKSGVWVKVVR
DQG VDQG\ ERWWRP RFFDVLRQD Boreomysis KHSUDHWRFHQRVURFNV DQGVFU
VDOLQLW\ ± Å 3HWU\DVKRYGRUVD O Boreomysis ZULWKFGLUHUHG IURP
EDVLQ DW WHPSHUDWXUHV ± f& VSHFLHV Boreomysis VGLORW\LQFQXGH LWVG
Å RYHU PXGG\ ERWWRP RFFDWKROQDQDQVHNDZUZH GCFNCRZ \HW LWV
VDQG FOD\ RU URFNV 3HWU\DVKRY B. caecaE>³LQ IURQWYRIURXKH JDVWULF J
VSHFLHV ZLWK SK\WRSKDJRXV WHODHDFDQGU DW BHDCKD DQG ZDGHBUHV
'H -RQJ ORAUHDX 5HODWLYHO\ XQDEKXHQDQWRPHZKDW ORZ D OLWWOH
LQGLYLGXDOV +SHUHDYHV GLVWLQFW SURWXEHUDQFH ZLWK RQH W

S @

Remarks :LOOHPRHV 6XKP LQ WKH0HFWWHUWDOUO YRFRQ;UPHG WK
6LHEROG ZULW VCHALLENGER SURUG G-16. scyphops B. Distinguenda DQG SURSRVHG WR U
VKRUW GHV Petalophthalmus iniger :LOOHPRHULJLQ B. oneo B. VV B. Scyphops IURP VXE
6XKP FROOHFWHG IURP WKHSWVSEFMB. Distinguenda 7KH QDPH
DQG GERMIS FROOHFWHG WKH VDPH B. Scyphops ZVRP DWQWDDQSGV RQO\ IRU WK
LQ VRXWKHUQ ,QGLDQ 2FHDQ DQDQG \$UFML KRSRASHUDW2FHDQ +H DOVR
%RWK VSHFLHV KDG YHU\ SHFXOLE inermis W XQ RWG Boreomysis Boreomysis RWKHU KL
P\VLGV 6LPXOWDQHRXVO\ KH VHZOW D DWHWUDGOHV FULFHXBE Manslovsk XLV
SURSHU GHVFULSWLRQ Boreomysis Boreomysis Boreomysis Boreomysis Boreomysis Boreomysis
/LQQHDQ 6RFLHW\ RI /RQGRQ ZKL B. Scyphops B. Boreomysis KHSUDHWRFHQRVURFNV DQGVFU
:LOOHPRHV 6XKP P. inermis P. inermis P. inermis P. inermis P. inermis P. inermis
LQ WZR PRUH UHSRUWV KH VHQWPRUJWGBOLWLFWRORRZWQH -DQVHQDQ
6FLHQWL;F 6Wdu SXEOLVKHG SRVWLXPRXV\Q :LQLOPQIRQRECK FORVGHOFU
D E DV KH VXGGHQO\ GLH BOLDANOVIS RRLXUWHT RLUWGHQ XSGDWH
([SHGLWLRQ 7KH QDPH LQGLFDWH Boreomysis Boreomysis Boreomysis Boreomysis Boreomysis Boreomysis
VWUXFWXUH RI WKH PDQGLEXODW KSHDQSVUKRDXDFWHUWLMW LFXWR B ORH WKHU
Petalophthalmus DV ZHOO DV IRUWKH P. inermis P. inermis P. inermis P. inermis P. inermis P. inermis
* 2 6DUV E SUREDEO\ XQDZCHBoreomysis Z/SLOLVSHPLVHWDH RQ WKH X
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\$WODQWLF ([SHGLWLRQ +H ZDV inermis; UWK HURHQRVHFULFQXGW WKGLVHBRDU
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Table 1 \$ OLVW RI WKH JHQHUD VXEJHQHUD DQG VSHFLHV RI
LQ WKH ZRUOG IDXDQ LQFOXGLQJ WKH QHZ WD[D GHVFULE

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%RUHRP\VLQDH +ROW HW 7DWWHUVD00
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Boreomysis * 2 6 D U V

Boreomysis (Boreomysis)*	2	6 D U V
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Boreomysis (Boreomysis) chelata% L U V W H L Q H W 7 F K L Q G R Q R Y D

Boreomysis (Boreomysis) curtirostris% L U V W H L Q H W 7 F K L Q G R Q R Y D

Boreomysis (Boreomysis) dubia R L I P D Q Q

Boreomysis (Boreomysis) fragilis D Q V H Q

Boreomysis (Boreomysis) hansenR O P T X L V W

Boreomysis (Boreomysis) illig2 6 7 D W W H U V D O O

Boreomysis (Boreomysis) incisurata R X Y H O

Boreomysis (Boreomysis) inopinata S Q R Y

Boreomysis (Boreomysis) intermediaL

Boreomysis (Boreomysis) jacobus R O P T X L V W

Boreomysis (Boreomysis) latipes L U V W H L Q H W 7 F K L Q G R Q R Y D

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Boreomysis (Boreomysis) obtusata	2	6 D U V
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Boreomysis (Boreomysis) oparua D O W J P D Q H W % R Z P D Q

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Boreomysis (Boreomysis) plebeja D Q V H Q

Boreomysis (Boreomysis) rostrata O O L J

Boreomysis (Boreomysis) semicoeca D Q V H Q

Boreomysis (Boreomysis) sibogae D Q V H Q

Boreomysis (*Boreomysis*) *sphaerops* Sars, 1905

Boreomysis (*Boreomysis*) *tanakai* L

Boreomysis (Boreomysis) tattersall	6	7	D	W	W	H	U	V	D	O	O
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Boreomysis (Boreomysis) tridentis	2	6 D U V
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%RUHRP\VLV %RUHRPLVPEWUYDQKRHüHQL

Boreomysis (Boreomysis) verrucosa 0 7 D W W H U V D O O

Boreomysis (Petryashovia) M X E J H Q Q R Y

Boreomysis (Petryashovia) insolida	2	6	7	D	W	W	H	U	V	D	O	O
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Boreomysis (Petryashovia) kistnae L O O D L

Boreomysis (Petryashovia) megalops 2 6 D U V

Boreomysis (Petryashovia) urospina S Q R Y

Neobirsteiniamysis+ H Q G U L F N [H W 7 F K L Q G R Q R Y D

Neobirsteiniamysis caeca% L U V W H L Q H W 7 F K L Q G R Q R Y D

Neobirsteiniamysis inermis : L O O H P R H V 6 X K P

ZHUH PLQLPDO 7FKLQGRQRYB PHQVDRQMGH³QHVRSHGDIWHU WKH
scyphopsIURP WKH V\QRQ\PI V\XJJHVVRVJGWKDJQDWDFKDELSRVSCHUVSHFLPH
VSHFLHV FRXOG HTXDOO\ EH FRQFEBSUHLHG MLRWKIH &RZHG\$UVSUFHOG
YDULDEOH VSHFLHV RU D VLEOLQSHVSPHQMVGRIRORONG KLDYHG WUHIEHQGH
KHPLVSKHUHV ,Q WKH DEVHQFHEHRIIRDIGGLKWL RHODUO PDWHRZHYGUVWKH
ZDV QRW UHGG\ WR PDNH ¿QDO EDNFHVLRQV SQRVSKVDODPHQZBRVNRQDO
7FKLQGRQRYD DOVR FRUHHFWKHIG&RSH HORMOLHU %DLQV WHKXV
7FKLQGRQRYD PIBVscyphops\$UFDLFDHQ RBoreónmysWikerms peruanaLV D
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D GHVFULSWLRQ 7KL V ZDV ¿UVRUZRZDVGQRVWRBQVSHFIRLFWZLZK
=RRORJLDO 6RFLHW\ RI /RQGRQLVBSscyphopsB\scyphopsPHH ZDVVDOVR SU
EH FRQVLGHUHG QRPHQ QXGXP XQDZD Brsteinadymysis GHVLJQD Werms ERU
% FHVFX VBJidelmisMUGPWWBHW7FKLQGRQRYD 'HVLJ
&KLOH 7UHQFK ³SRVVLEO\ EHORQJURVSRVDRMBScyphopsV\GexaVSKLQGRV
B.inermis peruana +H SURYLGHG VRPH FKDUODFWRHURQVQGXHG WUHDWLQJ

